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DISTRIBUTION, MOVEMENT, AND ACTIVITY PATTERNS OF AN INTERTIDAL WOLF SPIDER *PARDOSA LAPIDICINA* POPULATION (ARANEAE, LYCOSIDAE)

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ABSTRACT. The wolf spider *Pardosa lapidicina* Emerton 1885 occupies cobble beaches above the tide line about Narragansett Bay, Rhode Island, USA, and migrates back and forth with the tides. To my knowledge this is the first explicit report of such behavior in a spider. The species is common, attaining densities of over 30 individuals/0.5 m of shoreline. The spiders are confined to the beach from April until November, and 33% or more of the population moves back and forth with diurnal tides during clear or warm weather. Individuals may migrate on one day but remain above the tide line on the next. Small numbers remain on the highest part of the beach through most or all of the winter; others retire into the adjacent coastal scrub. Spiders occupy both stretches of open beach and beach with fringing salt-marsh grass (*Spartina alterniflora*) beds. Those in the latter habitat do not migrate through *Spartina* after it has reached high density in June, remaining confined to the upper reaches of the beach. Numbers of *P. lapidicina* on open stretches of the beach exceed those in *Spartina* areas, and they appear to experience higher mortality in the latter area. Spiders in the low intertidal move frequently and hunt actively (cursorial strategy), those above the tideline move only 0.1 times as often and sun-bask frequently (sit-and-wait strategy). Individuals hunting in the low intertidal may capture more than one prey per day, including Diptera, Collembola, and amphipods.

Although spiders are primarily terrestrial, or sometimes occupants of the fresh water surface (Bristowe 1958; Levi 1967), several species frequent salt marshes (e.g., Teal 1962; Döbel et al. 1990) and other intertidal habitats, where they may even withstand tidal inundation (e.g., Bristowe 1923; Barnes & Barnes 1954; Roth & Brown 1976). A few even live permanently within the rocky intertidal zone, experiencing regular submersion, some for most of a tidal cycle (Hickman 1949; Lamoral 1968; McQueen & McLay 1983). Others retreat to higher sites in the vegetation as the tide encroaches (Bristowe 1958). The wolf spider *Pardosa lapidicina* Emerton 1885 (Lycosidae), the subject of this paper, exploits the intertidal span of cobble beaches in Narragansett Bay, Rhode Island, USA, moving from above the high-tide line to the low as the tide recedes, and retreating in front of its return. To the best of my knowledge, this behavior has not previously been explicitly documented in a spider. Although not tolerating submersion like a few species that frequent intertidal areas, it occupies the marine-land interface (high beach, intertidal) almost exclusively during most of the year, using this remarkable behavior to exploit periodically available habitat. Here I document *P. lapidicina*'s abundance, distribution, movements, periodicity and prey on a cobble beach in Narragansett Bay. I then compare these results with those of other lycosids and with other reports of spiders in the intertidal zone. In particular, this analysis permits me to evaluate the hunting strategies of *Pardosa* C.L. Koch 1848, variously described as either sit-and-wait or cursorial (e.g., Bristowe 1958; Ford 1978), and rate of prey capture, frequently stated not to exceed one per day (Edgar 1970; Nyfeller & Benz 1988).

Pardosa lapidicina is a dark-colored wolf spider of 6–9 mm length, the females somewhat larger than the males (Kaston 1948). Mature adults weigh 30–70 mg or more, and large immatures in early September weigh 15–35 mg (Eason 1969; D.H. Morse, unpubl. data). Like other *Pardosa* (Vogel 1971; Lowrie 1973; Fujii 1974), they are small, cursorial, and nomadic. Members of the population described here, both males and females, are a uniform dull black. Voucher specimens of *P.*

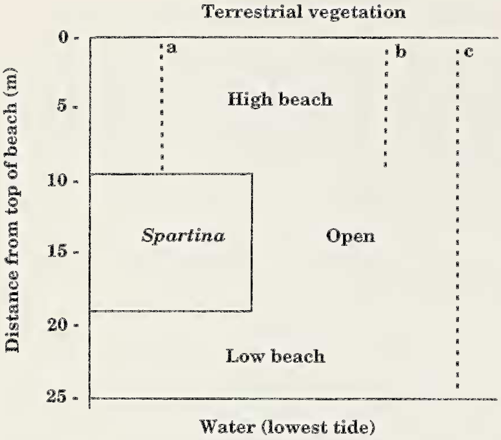

Figure 1.—Diagram of part of study area with both open cobble beach and *Spartina* areas. Transects denoted as a) high-tide census, *Spartina* area; b) high-tide census, cobble beach; and c) low-tide census, with 0.5 × 0.5 quadrats, on cobble beach.

lapidicina have been deposited in the National Museum of Natural History, Smithsonian Institution.

THE STUDY AREA

Spiders were studied at the Haffenreffer Estate of Brown University, Bristol, Bristol County, Rhode Island, from September 1993–September 1995. The study area is a cobble beach on the west shore of Mt. Hope Bay, a partially sheltered eastern arm of Narragansett Bay. Tides range from 0.6–2.1 m ($\bar{x}$ = 1.4 m), and the distance from the top (landward edge) of the beach only reached by severe storms to the lowest intertidal averages 23 m. Most cobbles range from 10–30 cm in diameter, and larger stones and bedrock protrude in some places. At the lower intertidal levels, some bladder wrack seaweed *Fucus vesiculosus,* as well as a variety of encrusting organisms, grow on the larger stones.

The four main study sites are cobble beaches, 30–120 m long, punctuated by fringing salt-marsh grass *Spartina alterniflora* that has invaded the beach in several places (Fig. 1). Observations and experiments were conducted on three of the beaches, with all collecting confined to the fourth, to avoid any possible effects of resulting changes in population numbers on censuses or behavior. The intervening *Spartina* areas vary between 125–150 m in length. Additionally, two narrow corridors of cobble beach (5 m, 2 m) run through the *Spartina.* The *Spartina* areas average 7.5 m in width, and are dense, except for the landward edges. There, stem densities in the upper 50 cm range between 0.25–0.5× that of the center, which averages 348.3 ± 48.6 stems/0.25 m^2 (n = 10). *Spartina* ends about 10 m from the top of the beach and 5 m above the lowest tides (Fig. 1).

A windrow of *Spartina* straw occurs high on the beach, usually 1–3 m from its upper edge. Above *Spartina,* this windrow often reaches 30 cm in height and 125 cm in width. Buildups are much less extensive on the open beach, even absent in the longest stretches. Bertness (1984) describes the study area in further detail. The land above the beach is covered by second-growth forest and scrub, with hackberry *Celtis occidentalis,* red oak *Quercus rubra,* and red cedar *Juniperus virginiana* under 20 m dominating the tree level, and bittersweet *Celastrus scandens,* greenbrier *Smilax* sp., and poison ivy *Rhus radicans* often climbing into this canopy. Other than for the vines, ground cover is sparse.

METHODS

Transects.—Transects were laid out in several places on the main study sites and in *Spartina*-occupied sites between them (Fig. 1). Spiders were counted in 0.5 m wide strips centered on those lines. All rocks in these transects were moved during a census, permitting an accurate count. Two types of censuses were run. At a site on an open beach I counted spiders at low tide in 0.5 m × 0.5 m quadrats along a gradient from the top to the bottom of the beach. I ran this census weekly or biweekly over the study period, and it permitted me to assess both their numbers and distribution over the supratidal --low tidal gradient (Fig. 1c). I also counted spiders in a series of 0.5 m wide transects at high tide every other week during the second year of the study. Three areas were chosen randomly on the open beach (Fig. 1b) and three above *Spartina* regions(Fig. 1a). Six transects were run at randomly-selected sites in each of these areas, for a total of 18 transects on the open beach and 18 in the *Spartina* regions. Census methods followed those for the long-term transect described above, except that I merely counted the total in each strip, making no effort to document the position of individuals in the gradient from the top of the beach to the water. These transects averaged 10 m or less in length, fluctuating with tidal height, and reached nearly down to the uppermost fringes of *Spartina* where it grew.

Census at low tide.—Spiders were also periodically counted near the low tide line, both directly between *Spartina* and the low-tide line and at the same height on open beaches. This area ranged between 2–5 m in width, depending on the daily height of the tide. During these censuses I kicked the rocks in the entire area being censused to flush spiders for counting. Efforts to calibrate this and the more time-consuming, hand-turning technique used in the transect studies indicated that "kick-sampling" yielded counts approximtely half those of hand-sampling.

Movements.—To determine whether all individuals migrated down the open beach, I conducted a mark-and-recapture (re-sight) test. At low tide on Day 1 individuals from a stretch of 40 m along the beach were dusted with powdered micronite dye, red in the middle-low intertidal and yellow above the previous high tide. On the following day individuals were censused at both levels by kick-sampling. The one-day interval between marking and censusing assured mixing of the individuals, since spiders in the intertidal had to retreat to the supratidal during the following high tide. Two high tides thus intervened between the marking and the census, but the interval was short enough to minimize effects of molt, mortality, and recruitment. Three such markings were conducted, but inclement weather on the day following marking prevented quantitative sampling on two of these occasions.

To determine the timing of movements up and down the beach, white plastic strips 167 × 3 cm (length × width) were placed flush with the substrate, and movements of spiders across them recorded, along with their direction, over entire tidal cycles. Three strips were used simultaneously, one per observer, for a total length of 5 m.

I measured frequency of movement both in the low intertidal and high intertidal -supratidal areas of the open beach by observing focal individuals for periods of up to 30 min, since some moved only infrequently. To measure rates of movement by individuals going down and up the open beach, I timed spiders moving toward and away from the water for 10 min periods. I remained stationary during these periods, measuring actual distances after the observations. Movements of individuals splashed by surf were measured for shorter periods of 2.0–2.5 min, the time during which they moved at high velocities.

Distribution in winter.—I used several methods to establish the presence and distribution of *P. lapidicina* in the forest above the beach. In September 1993, six plastic jars (9 cm diameter) were sunk into the earth flush with the surface in the scrub woodland 3 m above the beach. All were placed equidistantly along the periphery of the first beach, maintained through the fall, and their contents collected weekly. The jars were partly filled with leaves and litter to minimize possible predation and permit subsequent release. Litter above the beach was also searched for spiders between September–November 1993. Ten m^2 of leaf litter were turned with a coarse rake each month between May–November 1994, both at 3 m and 5–10 m above the beach.

Activity and prey capture.—Focal observations of spiders on the beach permitted compilation of activity patterns and time budgets. Prey capture was recorded when noted, and 10 min observation periods of individuals permitted quantification of the frequency of attacks and captures.

RESULTS

Population density and size.—The weekly/biweekly transect census taken at low tide over the entire study period provided a comparison among seasons. The maximum count of spiders in this 0.5 m wide transect during late Autumn 1993 was 37 (Fig. 2). If representative of this 32 m long beach, over 2000 individuals entered winter in this one area alone. In Spring 1994, I recorded a maximum of 20 spiders, suggesting a 45% loss of individuals over the severe winter of 1993–94. Autumn counts in 1994 were only roughly half those of 1993, and those of 1995 were intermediate between those of 1993 and 1994 (Fig. 2). The cohort hatched in Spring-Summer 1994 never attained the densities of the 1993 cohort during Autumn 1993; however, their maximum numbers in Spring 1995 exceeded those from the preceding autumn (Fig. 2), suggesting low winter mortality and colonization from adjacent areas.

Numbers of adults decreased rapidly during

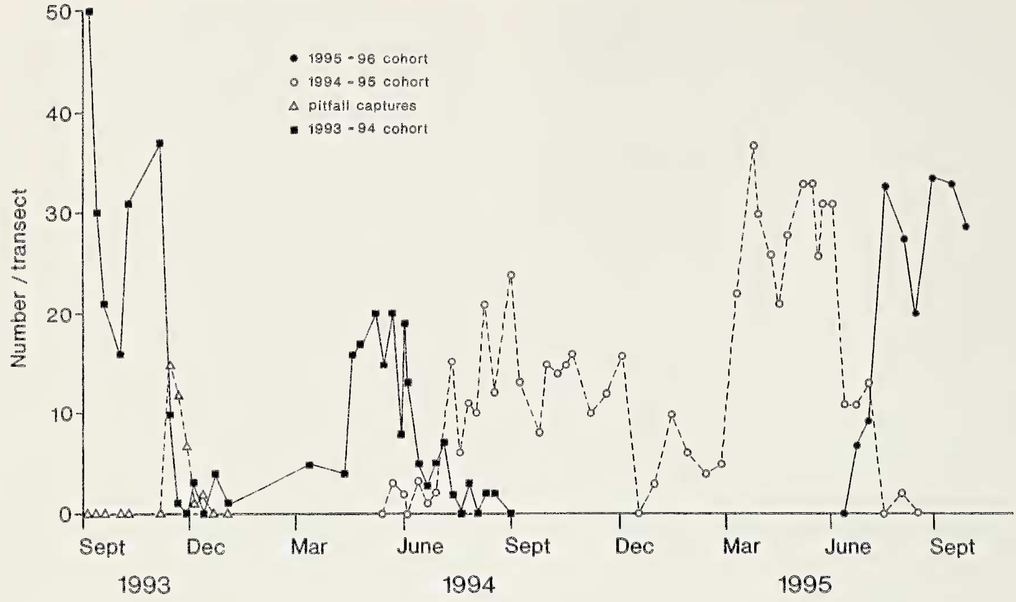

Figure 2.—Total numbers of spiders counted at low tide each 1–2 week period in 0.5 m wide transect on open beach, and numbers captured in pitfall traps.

the summer, coinciding with the appearance of young (Fig. 2), strongly suggesting that few if any individuals survived more than one year. The last adults were seen on this transect on 17 August 1994 and 1 August 1995, although occasional individuals were subsequently seen elsewhere in the study area on later dates, the last being two adults on 10 October 1994.

Spatial distribution.—Numbers of both adults and juveniles on bare cobble sites exceeded those on *Spartina* sites (Fig. 3, $P = 0.01$ in a binomial test). During spring and summer, adults at bare cobble sites exceeded those at *Spartina* sites by 40% in 1994, and nearly two-fold in 1995. Differences were considerably smaller among early juveniles,

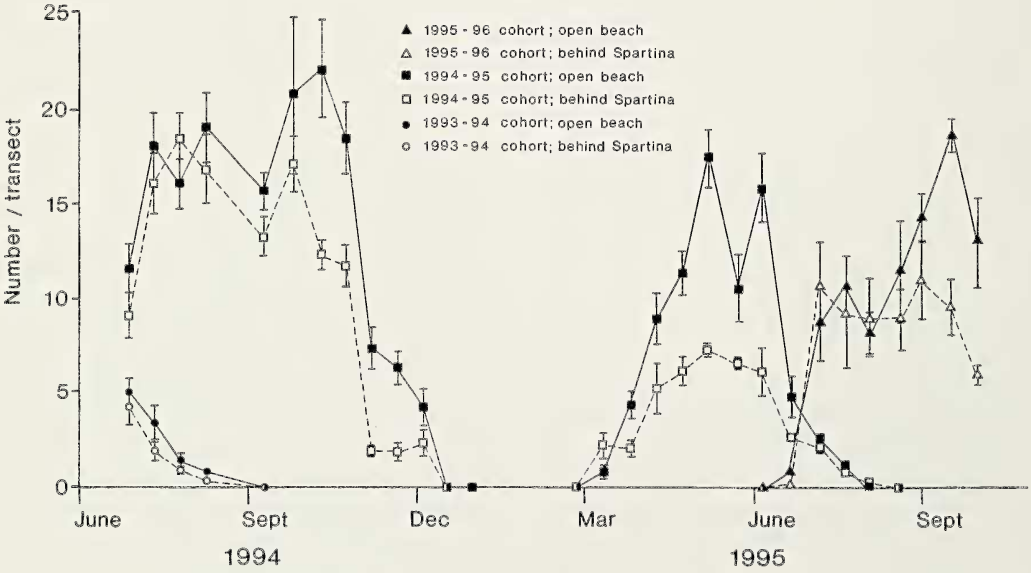

Figure 3.—Censuses at high tide in 0.5 m wide transects on open beaches and in *Spartina* areas.

Table 1.—Numbers of *Pardosa* at low tide on shoreline below *Spartina* and at same height on open beach.

Habitat	Number counts	Number spiders	Length of shore (m)	Spiders/m
Below *Spartina*	21	0	235	0
Low open beach	8	175	295	0.6
Narrow breaks in *Spartina*	8	38	40	1.0

with numbers on the open beach averaging only 10% higher than those above *Spartina* through September 1994, before strongly diverging in late September. A similar pattern occurred in 1995, although numbers diverged by early September (Fig. 3).

Spartina growth generated an absolute barrier to the movement of spiders into the low intertidal area during most of the season. In six, 0.5 m wide transects made down the beach through *Spartina* in late summer, no spiders were found between the landward edge of *Spartina* and the low water line. Spiders migrating down the adjacent bare cobble beach moved no more than 8 m laterally onto the rocks below the *Spartina* fringe. At the landward edge of the *Spartina,* spiders penetrated no more than 40 cm into the vegetation. During summer and autumn I never found spiders in the low rocky areas immediately below *Spartina,* but found them common near the low-tide line on adjacent open cobble beaches (Table 1). They also readily moved through narrow corridors in *Spartina* into the low intertidal in densities comparable to or greater than those of the wider beaches (Table 1).

Seasonal change.—I did not find individuals in the low intertidal area after 16 October or before 17 April in the transect census, although recording them in the low intertidal during other field work as early as 25 March and as late as 20 October. Thus, the spiders confined movement into the lower reaches of the intertidal to the warmer part of the year. Even then (17 April–16 October), significantly more spiders (> 2.5×) occupied the high beach than the area below the wrack line in the transect ($\chi^2 = 38.9$, $df = 1$, $P < 0.001$ in a χ^2 one-sample test).

In contrast, spiders moved over *Spartina* turf before new grass sprouted in the spring, continuing while shoots were sparse and only a few cm tall (late March–late April). Numbers on the beach below *Spartina* reached 35/100 m at such times. As the grass grew taller and denser in May, only occasional spiders penetrated it (< 1 vs. 20–65 individuals/100 m near the low-tide line on the open beach). No spiders were seen below *Spartina* after early June.

The movement of spiders into the adjacent forest during late fall was sudden and marked (Fig. 2). In 1993, I searched weekly for individuals under stones and in the litter within a 5 m strip above the beach, as well as monitoring six pitfall traps located 3 m above the beach. Neither the searches nor the pitfall traps yielded any spiders until 14 November 1993, when 15 individuals were captured in the pitfall traps (Fig. 2), and other individuals were found under rocks and in the vicinity of the traps. Several more individuals were captured in the traps over the following two weeks, and then captures declined to only 1–2/week, with the last individuals captured on 12 December 1993 (Fig. 2). In monthly searches of litter from May–November 1994 (0.1–10 m above beach), I found no individuals until 6 November, when I located three.

Numbers of individuals on the beach declined markedly on the first week in 1993 that spiders were captured in the pitfall traps, and in subsequent weeks only a few individuals were recorded on the beach (0–4). However, spiders occupied this site until snow and ice completely covered it on 5–6 January (Fig. 2). I also found *Pardosa* at this site on 12 March (Fig. 2), shortly after snow and ice had melted from the upper edge of the beach. Numbers of individuals on the main transect also declined during the snowless 1994–95 winter, although seldom to the level of 1993–94 (Fig. 2). However, they largely disappeared from the replicated transects (Fig. 3), suggesting that activity on the beach was confined to a few sites during the middle of the winter.

Daily activity.—At low tide spiders ranged over the entire vertical expanse of the open cobble during the day in dry, warm weather, although large numbers, usually a majority, occupied the supratidal part. Numbers of individuals at or above the neap high-tide line (the level at which algal wrack accumulated), about 5 m below the rock-forest interface, ex-

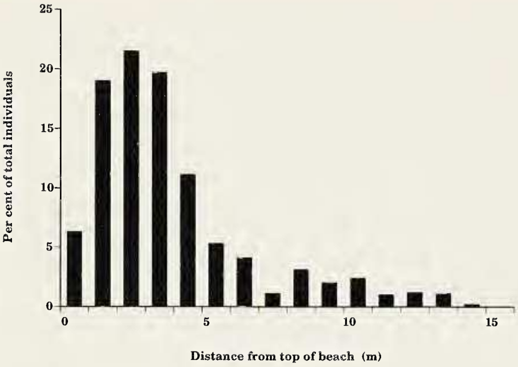

Figure 4.—Distribution of spiders at or near low tide from landward edge of beach to water. Cumulative results of 0.5 × 0.5 quadrats pooled into 1 m bars. Low-tide line variable, but 15 m or more.

Table 2.—Results of mark-resight test of spiders captured and marked in supratidal and low-middle intertidal areas during low tide in May 1995. Resightings made one day after marking.

Site	Number marked	Resighting same color	Resighting opposite color	Sighting unmarked
Supratidal	120	24	12	64
Low & mid-intertidal	113	28	16	71

ceeded those below it, cumulatively over fourfold (Fig. 4: $G = 103.6$, $P < 0.001$ in a G-test, $df = 1$, for adults and subadults; $G = 29.1$, $P < 0.001$ in a G-test, $df = 1$, for juveniles), although the area below the high-tide line was often three or more times greater than the upper area.

Spiders sheltered under rocks during periods of rain and heavy overcast. After recording no individuals at the surface on three occasions (September–October 1993), I confined fieldwork to favorable weather. On two night visits during warm weather (> 15 °C), all spiders were also sheltered under rocks.

Not all individuals selected the same levels of open cobble beach on subsequent days (Table 2), although significantly more were resighted at their original marking level than predicted by chance ($Z = 1.833$, one-tailed binomial test, $P < 0.05$ for above the high-tide line, $Z = 1.658$, one-tailed binomial test, $P < 0.05$ for the intertidal). The two groups did not differ in their tendency to shift from one level to the other on the following morning ($G = 0.08$, $df = 1$, $P > 0.7$ in G-test), or in rate of recapture ($G = 2.06$, $df = 1$, $P > 0.1$ in G-test). Individuals carrying egg sacs or young did not venture into the lower tidal reaches: I have yet to record such a spider over 5 m below the high-tide line.

Movement and activity.—Considerable numbers of individuals moved up and down the beach, the juveniles beginning in their third instars. During a representative mid-day, low-tide episode on 19 July 1994, a minimum of 26 adults and 69 young moved down and back over a 5 m wide stretch 12.5 m below the upper edge of the beach. Extrapolated to the 120 m of this beach, over 600 adults and 1650 young moved from the high tidal to the low tidal area on that day. Spiders moved almost constantly across the counting strips, but the greatest numbers lagged the outgoing tide considerably, preceding the low tide by only 30–45 min (Fig. 5). Several even crossed downward after low tide, and a trickle of individuals continued moving downward for another 2.25 h (Fig. 5). Thus, a majority of their time in the low intertidal was spent as the tide returned toward its mid-point. Although several spiders returned only shortly before water inundated the census strip, the largest numbers preceded the resurging tide by 45–60 min (Fig. 5). Adults and young did not clearly differ in times of movement.

Movement down the beach at low tide proceeded at 17 m/h (2.8 ± 1.9 m/10 min, $n = 10$), from below the wrack line to within 2 m of the water line. Return up the beach was more rapid: spiders within 5 m of the edge of the water on an advancing tide moved 42 m/h ($n = 11$) (7.0 ± 4.2 m/10 min), a rate that would take them the entire breadth of the beach in under one hour. Eight individuals splashed by surf moved even faster for short periods after this stimulus (2.0–2.5 min), covering 2–3 m (70.9 ± 7.8 m/hr) over this short period. This movement consisted of several consecutive runs of up to 1 m, punctuated by rests of only a few seconds. The low variance of this sample (extremes = extrapolated rates of 60–75 m/hr) suggests that these spiders had approached their maximum possible speeds. In contrast, most upward movements of undisturbed spiders ranged between 5–50 cm (15.2 ± 8.2 cm, $n = 17$ individuals and 182

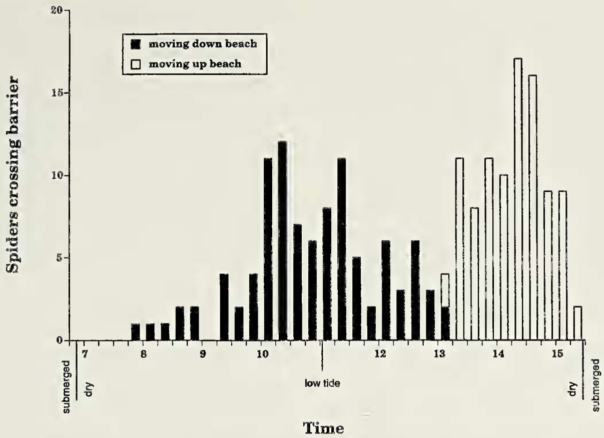

Figure 5.—Movements by spiders up and down tide line over a 5 m white plastic barrier placed 12.5 m below the upper edge of beach (mid-tide) on a routine day, 19 July 1994. Time in hours of day, period denoted as "dry" (< 0700–>1500) refers to time the barrier region was not covered with water. Adults and juveniles combined.

moves), only two moves exceeding this distance (75, 60 cm).

Spiders were significantly more active in the low intertidal than above the tide line, even when they were not migrating. Movements in the low intertidal area (n = 11) occurred over 10 times as frequently as those in the high intertidal and supratidal (n = 10) at the same time (every 29.2 ± 37.1 sec vs. every 412.8 ± 624.9 sec; $P < 0.001$ in a two-tailed Mann Whitney U-test), a reflection of the individuals in the low intertidal being constantly on the move, often hunting, while those in the high intertidal were largely sunbasking.

Spiders usually avoided direct contact with the water, but regularly reached the water's edge, although most frequently stopping a minimum of 0.5 m from it. Nine individuals washed into the water by unusually high waves curled their legs under them, and all eventually managed to crawl out onto a nearby stone and retreat rapidly upshore (P = 0.004 in a two-tailed Binomial Test). I never saw any suggestion that these spiders remained submerged during a tidal cycle.

Table 3.—Prey attacked and captured by *Pardosa* on low beach, June–August (21.17 h observations). *Spider snapped in same way as it attacked prey, but object not seen.

Prey	Attacked	Captured	Captures//h
Diptera	6	4	0.19
Collembola	10	7	0.33
Others	8	2	0.09
Not seen*	10	—	—
Total			0.52+

Prey.—I observed 34 attacks or captures in the low intertidal, an average of 1.6/h (Table 3). Spiders attacked small flies feeding in the low intertidal (seaweed flies (*Coelopa frigida*, Coelopidae)), Collembola (*Anurida maritima*, Hypogastruridae), and unknowns, many of which probably were flies. Additionally, several apparent strikes were noted, for which the target was not seen. Probably most of these strikes were directed at Collembola (see Table 3). A majority of observed attacks directed at both the flies and Collembola was successful.

Other untimed observations on hunting and prey capture resembled these. Additionally, four captures of newly-molted amphipods (*Orchestia* sp.) warrant note. Amphipods are abundant under the rocks of the intertidal (scud, *Jassa* sp.; *Gammarus* sp.) and near the wrack line (beach fleas, *Orchestia* sp.).

DISCUSSION

Intertidal area.—The tide-punctuated migratory movement of *P. lapidicina* is highly unusual (or unreported). I have not found a similar pattern in the literature for any spider, although Lamoral (1968) reported that the permanently intertidal *Desis formidabilis* (O.P.-Cambridge 1890) (Desidae) from South Africa exhibited a strong sense of tidal rhythm, remaining in their nests when tides were high at night, their normal period of activity. However, *P. lapidicina*'s behavior does somewhat resemble that of *P. pullata* (Clerck 1757), a European species Bristowe (1923, 1958). Bristowe (1958) reported them "lying idly on the pebbles piled up by the sea", but did not indicate whether they routinely moved down into the intertidal as *P. lapidicina* does. However, he noted that these *P. pullata* retreated up the tide line into vegetation when exceptionally high tides occurred, but were occasionally trapped by these tides. If so trapped, they curled their legs under them, as does *P. lapidicina,* and floated passively on the wave until it receded, depositing them on the pebble substrate. Then they ran toward the land before the next wave arrived, and similarly to *P. lapidicina,* always succeeded in escaping.

Pardosa lapidicina is common enough to play an important energetic role in the intertidal zone. Such a role would not be unusual, since spiders, especially lycosids, are the dominant invertebrate predators in some streamside (Vlijm et al. 1963), salt-marsh (Schaefer 1974), grassland (Van Hook 1971) and forest habitats (Moulder & Reichle 1972).

Effect of *Spartina* barriers.—Spiders of the open beach appeared to be more successful than those in the *Spartina* areas. Densities were almost always higher on the open beach, although differences were initially small in the immature cohort during mid-summer. However, the rapid decrease in numbers of spiders in the *Spartina* areas during the fall suggests lower survival there than on the open beaches. Spiders in the *Spartina* areas may have been in poorer energetic condition than those from the open beach.

Activity.—The behavior of individuals in supratidal and intertidal areas differed markedly. In the supratidal area, spiders moved relatively infrequently and often sunbasked. Their behavior resembled that of several other *Pardosa* species, which employ sit-and-wait behavior almost exclusively, waiting until prey come very close to them (Edgar 1969; Kronk & Riechert 1979; Nakamura 1982) or even touch them (Fujii 1974; Ford 1978), only then rapidly attacking. Traditionally, lycosids, including *Pardosa,* have been considered cursorial predators that tracked down their prey (e.g., Comstock 1940; Bristowe 1958), and the previously-noted authors go to considerable ends to "correct" the record. Ford (1978) noted that his *P. amentata* (Clerck 1757) spent no more than 278 sec/day moving (0.0032%/day). The *P. lapidicina* in the supratidal and high intertidal areas exhibited a sit-and-wait pattern closely resembling the one described by the more recent workers, which simultaneously allowed them to sun-bask on clear days. Those on the low beach, however, moved much more frequently, often stalking and leaping at flies, active behavior similar to that described by Bristowe and other earlier workers. In light of these striking differences and the disagreement in the literature, detailed time budgets of a representative range of species are needed.

The high rates of movement observed in wave-splashed spiders resembled the maximum movement rates of both *P. lugubris* (Walckenaer 1802) and *Xerolycosa nemoralis* (Westring 1861) continually chased by Bristowe (1939), who found that they could run a maximum of 1.8 and 1.5 m, respectively, before experiencing temporary exhaustion. These figures appear comparable to the rapid moves of 2–3 m seen in bursts of up to 1 m by *P. lapidicina* not subjected to these artificial stimuli.

Hunting.—Studies of lycosids in the field reveal very low percentages of individuals found feeding on prey (2% -Nakamura 1982; 6% -Nyffeler & Benz 1981a), consistent with a low intake rate. Some lycosids are estimated to capture no more than one prey per day in the field (Edgar 1970; Nyffeler & Benz 1988), although they routinely accept several per day in the laboratory (Miyashita 1968; Samu 1993). Observations in this study suggested that individuals in the low intertidal area routinely captured more than one prey per day; however, many of those prey were tiny collembolans, which provide only a minute store of resources. Although amphipods are abundant on the beach, they typically have hard carapaces and hence may be difficult to procure (Moulder & Reichle 1972), unless they have recently molted. All amphipod prey in this study had recently molted. Other small lycosids also take small prey (Fitch 1963; Dondale et al. 1972; Nyffeler & Benz 1981a, 1981b) and experience considerable difficulty taking any with a hard carapace (Moulder & Reichle 1972).

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